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Population Variability and Apparent Recent Decline of River Birds in the Indian Himalaya

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ABSTRACT

Abundance estimates are critical to animal conservation in the tropics and sub-tropics, but assessments for some species and ecosystems in these regions are poorly developed. Estimates are particularly scarce for subtropical mountain rivers where some river organisms reach their greatest global diversity while being at risk from global change. We addressed these issues along rivers in the western Indian Himalaya, focusing on 12 bird species with varying dependence on river production, distribution, abundance, and detectability. We estimated river bird abundance through repeat field counts across 5 years using N-mixture models to correct for imperfect detection from sparse data over an altitudinal range of 330–3100 m. Estimated abundances were modeled against elevation, flow, and river width as covariates. Detection probabilities overall were greatest in flycatching insectivores connected closely to the river channel and lowest in two piscivorous kingfishers. Patterns of abundance also varied among groups particularly in relation to elevation, with river passerines mostly recorded at mid and higher elevations and piscivorous taxa recorded mostly below 1600 m a.s.l. Five species apparently declined in overall population size by 5%–10% across the 5-year study, in three cases matching national scale trends recorded by citizen science platforms. Our results reveal the utility of open *N*-mixture models in assessing population trends of specialized river organisms in subtropical mountain environments where high-resolution data are difficult to collect. The data also hint at possible threats to Himalayan rivers that could affect this globally unique community of river birds.

1 | Introduction

Rivers globally are at risk from large-scale anthropogenic change through habitat modification, hydrologic alterations (e.g., hydropower development), diffuse and point-source pollution, climate change, and introduced species (Gergel et al. 2002; Rashid and Romshoo 2013; Sinha et al. 2019; Vercruysse and Grabowski 2021). With impacts on global river biodiversity already pronounced (Humphries and Winemiller 2009; Vörösmarty et al. 2010; Elosegi and Sabater 2013), regular monitoring of key indicators is vital in guiding river conservation and restoration (Karr 1999; Calderon et al. 2023). As well as assessments of freshwater species, organisms in the wider river corridor can reveal a range of changes through trends in population or other life-history measures (Gergel et al. 2002; Gomez-Salazar et al. 2012;

Eriksen et al. 2021). This is because they can integrate conditions across the riparian zone or catchment as well as in the river's wetted perimeter (Maznikova et al. 2024).

Headwater streams are crucial components of river networks that have important ecosystem functions both locally by providing specialized habitats and longitudinally by influencing downstream conditions through fluxes of solutes, matter, and energy (Ward et al. 2002; Wohl 2017). As with other river segments, they are at risk from local and global change, for example, in climate, land use, and resource exploitation (Riley et al. 2018; Jacobsen et al. 2024). This is particularly true for the major subtropical and tropical rivers that originate in the Himalayan mountains, which simultaneously support some of the most diverse river ecosystems on Earth alongside some of the greatest and most rapidly growing human populations (Immerzeel et al. 2010).

Among this rich diversity of flora and fauna, specialist river birds are not only integral to the ecological dynamics of Himalayan streams and rivers but also reach their greatest richness in this region as a consequence of high relief, ecosystem productivity, and phylogenetic diversification (Buckton and Ormerod 2002). Although there are many freshwater birds globally (Ormerod and Tyler 1993), specialized river species like those in the Himalaya have been defined specifically based on criteria reflecting their (i) use of production from the river channel either by direct aquatic foraging or by exploiting the prey subsidy exported from the river channel, for example as flying insects; (ii) occupancy of habitats for most of their life cycle that have been created specifically by the fluvial geomorphology of high-energy rivers; and (iii) straightforward observation and quantification in generally linear territories along river channels (Sinha et al. 2022). These criteria make them distinct from bird species, for example, in riparian forest or in other freshwater ecosystems (Stauffer and Best 1980; Knopf 1985; Robinson et al. 2002; Sinha et al. 2019). Previous studies in the Himalaya have shown that specialist river birds partition habitat space such that species are segregated ecologically, for example, among different elevations, river flow types, and different parts of the channel (Buckton and Ormerod 2008; Sinha et al. 2019). Foraging niches also vary because the community includes piscivorous species, several insectivorous species that feed either on river insects in either their aquatic or aerial adult stages (Murakami and Nakano 2002; Iwata et al. 2003; Buckton and Ormerod 2008; Sinha 2021).

For all the above reasons, specialist river birds are prominent candidates for monitoring and assessment in subtropical headwaters and tropical catchments (Vaughan et al. 2007; Figarski and Kajtoch 2015; Sinha et al. 2019). Evidence shows already how specialist river birds can indicate environmental changes across multiple scales and through different ecological pathways (Bryce et al. 2002; Vaughan et al. 2007; Larsen et al. 2010; Sinha et al. 2019), and some bird species are already established as flagship river indicators (Maznikova et al. 2024). However, despite apparently widespread and substantial population declines among populations of other riverine vertebrates (Quaglietta et al. 2018; Gomez-Salazar et al. 2012; He et al. 2019), river birds have attracted less attention from animal conservation biologists (Norbury and Heyward 2008).

Despite existing knowledge, further assessments are needed to develop long-term monitoring schemes for river specialist birds in tropical and subtropical regions to further understand links between population trends, changes in river ecosystems, and options for conservation. Although population estimates over space and time serve as an important foundation for understanding species response to environmental change (Kéry 2008), there are some constraints on the collection and use of field population data that are particularly pronounced in the tropics and subtropics. While periodic density estimates might be used to monitor species population trends (Gregory et al. 2004, 2007; Collier et al. 2013), robust estimates of bird population size are challenging to produce in these regions for two principal reasons. First, bird numbers fluctuate across seasons and from year to year as individuals breed, die, and migrate (Newton 1998). Logistical issues mean that a full census (i.e., counting every individual) is practically impossible, especially in inaccessible locations and for species that are naturally rare or mobile. Researchers therefore must rely on data gathered across a sample of sites or times and use statistical techniques to build population estimates from sample data (Dénes et al. 2015). This creates inevitable assumptions and uncertainties that affect the accuracy of population estimates (Hewson et al. 2018). Second, the detectability of target species in the field varies between times and locations. The assumption that individual animals are present or conspicuous throughout the entire duration of a field survey is often not realistic (Fogarty and Fleishman 2021). In most instances, birds cannot be counted with certainty in the field, as the chances of missing individuals vary with multiple factors that cannot be controlled (Kéry et al. 2005; Buckland et al. 2008; Kéry 2008). Detection is heavily dependent on the habitat being surveyed, the survey design, the behavior or life stage of the species, and the survey conditions which might vary from one sampling window to another (Conway and Gibbs 2011; Diefenbach et al. 2003; Pacifici et al. 2008; Banks-Leite et al. 2014; Iknayan et al. 2014). Hence, there is a need to account for detectability when attempting to estimate unbiased counts of species from field data (Dénes et al. 2015).

One possible approach to addressing these issues is the use of N-mixture models, which can produce density estimates across years to estimate population variability (Dail and Madsen 2011). They can provide a cost-effective alternative for estimating detection probability and population size from field surveys without the need to identify or capture and mark individuals (Royle 2004). The model is easy to describe and implement and can be fitted for a wide variety of field sampling studies where data come from repeated counts at a series of sampling sites (Dennis et al. 2015). N-mixture models have been used effectively for population estimation of birds spanning different families and in different environments, although few involve rivers (Kéry 2008; Joseph et al. 2009; Goldstein and de Valpine 2022; Duclos et al. 2019; Zou et al. 2019). In this respect, rivers and specifically river birds in subtropical or tropical mountain regions where comprehensive surveys are challenging are a valuable system in which to explore the N-mixture approach.

In this study, we apply N-mixture models to estimate the detection probability and population abundance of river birds in the Himalaya using a dataset collected across multiple years. We anticipate that monitoring spatial and temporal trends among Himalayan river bird populations can provide key insights into habitat quality both locally along specific reaches or tributaries and also more extensively across mountain areas where these species occur. Similar monitoring schemes have already been developed for river birds in other regions of the globe (e.g., Vaughan et al. 2007).

We asked the following questions: (a) What are the population trends of breeding river birds across years? (b) Do the trends differ for obligate and non-obligate river birds—respectively those with more and less fundamental ties to river production? (c) How do environmental covariates shown to be important previously for river birds (i.e., elevation, river-width, flow: see Sinha et al. 2019; Maznikova et al. 2024) influence the estimated abundance of these species? Our intention is to contribute specifically to river conservation through monitoring river-dependent bird species in the Himalayan mountains (Manel et al. 2000; Sinha et al. 2019). A further objective is to examine the applicability a particular analytical model that may have wider application across logistically challenging tropical and subtropical locations.

2 | Methods

2.1 | Study Area

Field data were collected in the Bhagirathi basin, an important headstream of the Upper Ganges in the state of Uttarakhand in the western Indian Himalaya, and six associated first-order streams. The sampled sites encompassed an elevational gradient between 3100 m a.s.l. (30°59′39.1″ N, 78°56′38.7″ E) and 330 m a.s.l. (30°07′03.9″ N, 78°18′26.0″ E) (Figure 1). The main headstream flows through deep gorges and narrow valleys in the upper reaches except one stretch where the river broadens into a valley with braided, shingle riverbeds. Major tree species in the riparian tracts include broadleaves, conifers, and some riverine specialists (Sinha et al. 2019). Human settlements range from small to medium suburban locales and many small hamlets. The major settlements include Rishikesh (300 m a.s.l.), Devprayag (700 m a.s.l.), New Tehri (2100 m a.s.l.), Uttarkashi (1300 m a.s.l.), Harsil (2500 m a.s.l.), and Gangotri (3200 m a.s.l.) (Figure 1). This basin was chosen as it provides a large elevational gradient while typifying variations across the Himalaya in natural vegetation and human land uses including deforestation, road building, human encroachment, and dams for hydropower (Rajvanshi et al. 2012). The river Bhagirathi has large

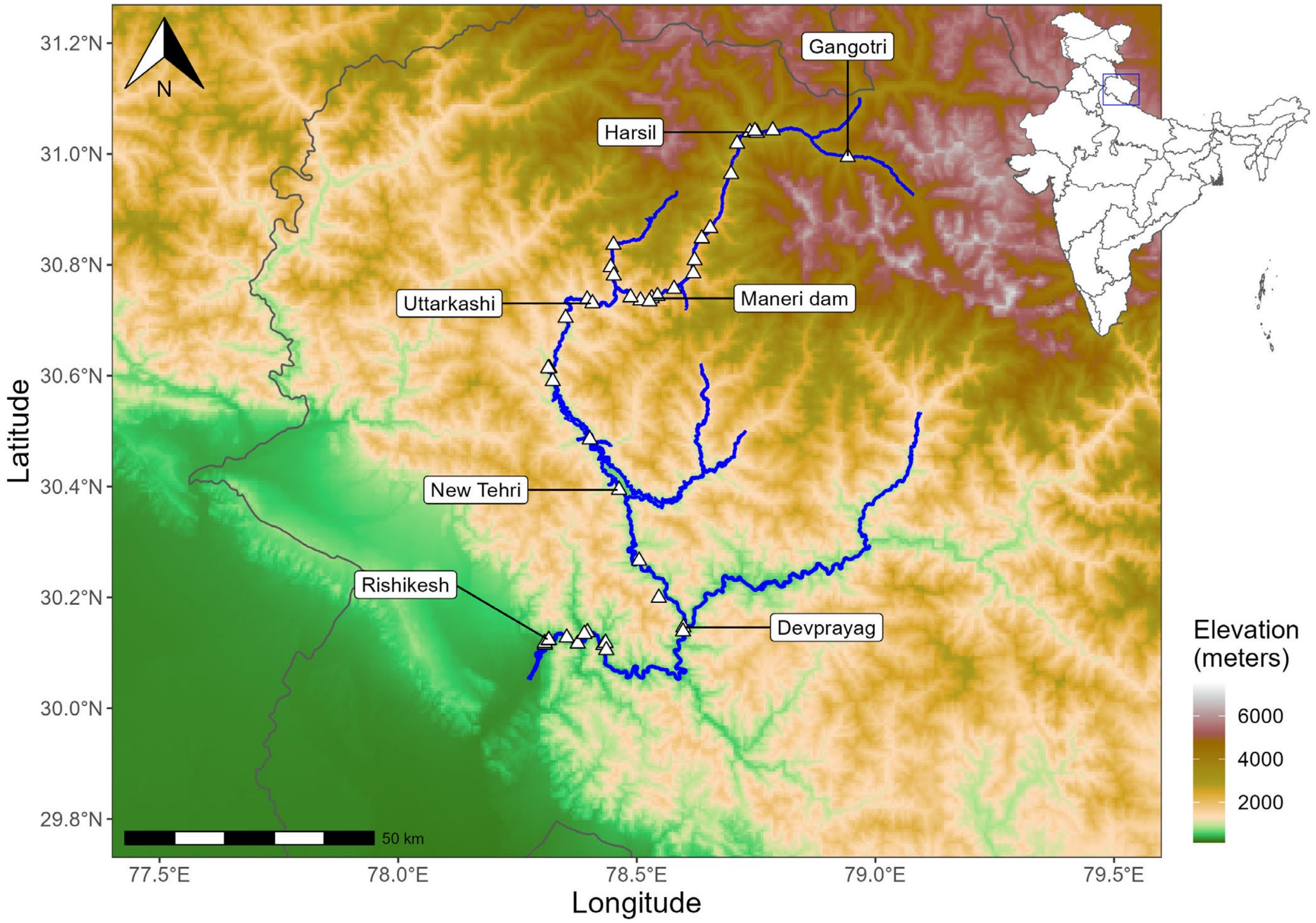

FIGURE 1 | Map showing the Bhagirathi basin in the state of Uttarakhand (blue box) in India (inset). The white points depict the midpoint of every 500 m river reach surveyed for river birds along the elevation gradient.

hydropower potential and functional dams along the river that include Maneri, Joshiyara (Bhali), Koteshwar, and the Tehri (Rajvanshi et al. 2012). Impacts include altered flow regime, diverted river length, and submergence of land with forested areas and human habitation (Gaur et al. 2019). These are recognized pressures on river ecosystems known to affect river bird distribution in the Himalaya (Vaughan et al. 2007; Sinha et al. 2019, 2022).

Runoff in this system arises from different sources that range from glacial melt, rainwater, and groundwater springs. During the sampling years, summer months were short at the higher elevations (above 2000 m a.s.l.) and lasted from April to June, when days were typically clear with occasional light showers (above 2500 m a.s.l.) giving way to major rainfall during the monsoon from July to September (Sinha 2021). At elevations below 700 m a.s.l., summer temperatures surpassed 40°C in the month of May with cooler temperatures at higher elevations.

2.2 | Field Survey Design

Forty-three river reaches of 500 m were surveyed in the years 2014–2018 along an altitudinal gradient between 300 m and 3100 m a.s.l. following a widely used model for assessing river bird distribution (Buckton 1998; Figure 1). Surveys were carried out in the summer months between the end of March and mid-June, which precedes the monsoon but spans the prime breeding season for all the species except Brown Dippers (*Cinclus pallasii*), which breed between December and early August. Three visits were made to each river segment (500 m) in each year to increase the detection probability of all species (McCarthy et al. 2013) following previous assessments for bird species that occupy linear territories along rivers (D'Amico and Hemery 2003). Abundances were estimated as numbers of birds per 500 m for each species. The pattern of visits to each region was randomized as far as logistically possible to avoid spatiotemporal auto-correlation in the resulting data. Bird surveys were conducted by the same observer by walking along the banks during early morning (06.00 to ±10.00) and late afternoon (15.00 to ±18.00). All birds seen using 8 × 42 binoculars were identified and recorded if they occurred within 100 m of the wetted perimeter, for example in flight, but in practice, most were in the channel or immediate riparian zone (Marchant et al. 2002). A species was recorded as present if it was observed during surveys on any occasion (out of the three visits) and considered absent otherwise.

River Habitat Surveys were undertaken simultaneously with every bird survey to capture information on river channel structure, flow character, bank structure, riparian vegetation, and adjacent land use using a blend of categorical and ordinal variables. This approach followed methods developed initially in Europe (Raven et al. 1998; Vaughan et al. 2007) that were applied subsequently in Nepal and India (e.g., Manel et al. 2000) and refined for the current study (Sinha et al. 2019). In outline, the method involves categorizing the character of the river channel, the banks, and the riparian zone on a six-point scale. Elevation was recorded in the field through a handheld Garmin eTrex GPS; recordings were taken at the beginning and the end of the 500 m section; and an average was taken for that section. River width was calculated through measuring Euclidean distances between wetted perimeters of both banks at all the six points in Google Earth Pro and then averaging for the 500 m sections. River flow was classified as cascades, riffles, runs, and dam backwaters with respective scores of 3 (= abundant features), 2, 1, and 0 (= no features present). Observations were made at each of the six points across the 500 m sections and averaged for a flow score for that river reach. Although other river habitat variables were collected simultaneously during field surveys (details in Sinha et al. 2019), only three showed significant variability across the sites where bird species were detected across the 5 years of field sampling and thus had significant effects in predicting the presence/absence of the 12 river bird species. Only these three variables were used in the final model to estimate the modeled abundances of bird species.

Birds were grouped into two categories (river obligates and non-obligates) depending on their dependence on river production. River obligates were defined as species that (a) occur exclusively along streams or river channels during a significant part of their breeding or non-breeding life cycle; and (b) depend on production wholly or partly originating from the river channel (Buckton and Ormerod 2002). Species feeding and roosting in habitats such as wet woodlands, inland waters, ponds, and lakes besides inhabiting river banks were described as non-obligate species.

Field data from replicate surveys spanning 5 years (summer: 2014–2018) were used to understand population variations across time. Any species occurring in fewer than five river reaches were not considered for further analysis. The number of individuals of each species was recorded per river reach (500 m). We also compared the population variations of the target species from the study area with long-term and current annual trends from the State of Indian Birds SoIB, 2023 (https://stateofindiasbirds.in/) to form a holistic overview of the long-term population status for these species across their range in India.

A total of 32 bird species from 12 families were found using riparian areas of the Bhagirathi river during the 5-year survey period (Table S1, Sinha 2021). We chose 12 species (6 obligate riverine and 6 non-obligate riverine birds) recorded at least once on all occasions of sampling across more than five sites for this analysis. We used a study design of replicated counts to estimate the species population using an N-mixture model (Royle 2004). The design followed the assumptions of the N-mixture model and observed counts $n_{i,t}$ of distinct individuals of riverine birds at sites $i = 1, \dots, S$ $(S = 43)$ during $t = 1, \dots, T$ $(T = 3)$ primary sampling occasions, where the populations within each of the S sites are assumed closed (no births, deaths, immigration, and emigration) during the T occasions. We used the design for each year and incorporated the dynamic N-mixture model for open population (Dail and Madsen 2011) to follow the non-closure assumption of the metapopulation. Along with that non-closure assumption, we also used additional assumptions of independent detections and constant detection probability p.

The initial observed counts follow an observation process described by:

$$n_{i,t} \sim \text{Binomial}\left(N_{i,t}, p\right) \tag{1}$$

with N_i being the size of the population at site i.

Furthermore, we assumed that the latent abundance distribution follows either a Poisson or a zero-inflated Poisson (ZIP) distribution.

$$N_i \sim \text{Poisson}\left(\lambda\right) \quad \text{or} \quad N_i \sim \text{ZIP}\left(\lambda\right) \tag{2}$$

Furthermore, we used different site covariates to model the spatial variation in the site-wise count.

$$\begin{aligned}\log\left(\lambda_i\right) = \beta_0 + \beta_1 * \text{elevation}_i \ + \beta_2 * \text{flow} - \text{character}_i \\ + \beta_3 * \text{width of river}_i\end{aligned} \tag{3}$$

Using the open population N-mixture model framework described above, we further estimated the population sizes N_i for every site and the total population size $\sum_{i=1}^{S} N_i$ for every sampling occasion.

We used the dynamic N-mixture model described by Dail and Madsen (2011) to model the annual change in population between sampling occasions. The estimated population $\left(N_t\right)$ for every year is modeled as a sum of two random variables (surviving population $S_{i,t}$ and new individuals $G_{i,t}$). S_{ij} is the number of individuals at location j that survive from the previous year (t–1) to t and remain at j. G is the number of individuals that were gained either by migration or immigration at location j between times t–1 and t. The population growth can be parametrized by multiple ways (e.g., constant recruitment, exponential growth, auto-regressive growth, density-dependent growth) based on the species ecology and habitat. We used an assumption of auto-regressive model, where the current year population depends on the surviving individuals from previous year and new recruits. As the species' habitat are mostly restricted by resources from linear habitats, we fit an auto-regressive model over other growth models. The abundance $\left(N_{i,t}\right)$ at each site for $(t > 2)$ is modeled based on the abundance of previous year $(N_{\mathrm{i},t-1})$ and is described as a first-order Markov process. Hence,

$$S_{i,t} \mid N_{i,t-1} \sim \text{Binomial}\left(N_{i,t-1}, \varpi\right) \tag{4}$$

$$G_{i,t} \mid N_{i,t-1} \sim \text{Poisson}\left(\gamma\left(N_{i,t-1}\right)\right) \tag{5}$$

where ϖ is the apparent survival probability of individuals and γ is the arrival rate of individuals dependent on the population's local abundance. The total population abundance at a location in time t is modelled as

$$N_{i,t} = G_{i,t} + S_{i,t} \tag{6}$$

All the models were fitted with a maximum likelihood framework using the "pcountOpen" function of the "unmarked" package (Fiske and Chandler 2011). The "pcountOpen" function gives the user the ability to customize the numerical optimization by choosing the finite bound (K) used to approximate the infinite sums in the likelihood. The K value is supposed to be set in such a way which should be less than the estimated population for the sites. We used $K = 50$ for all the models. We used chi-squared goodness-of-fit and c-hat values to evaluate the model fit and overdispersion with 1000 simulations for each bird to calculate the chi-squared test statistics. All statistical analyses were performed in R 4.2 (R Core Team 2024).

3 | Results

We recorded 3307 individuals of our 12 target bird species across 43 sites during the summer breeding months. Blue Whistling-Thrush followed by Brown Dipper were recorded across the maximum number of sites (Table 1). Overall, for the 5 years, Plumbeous Water Redstart was the most abundant species while Little Forktail was the least abundant (Table 1). Detection probability varied across species, being highest for Plumbeous Water Redstart among obligate species and for Grey Wagtail among non-obligates (Table 1). White-throated Kingfisher followed by the Common Kingfisher had the lowest detection probabilities.

For all the species, AIC values for both the Poisson and the zero-inflated Poisson models were mostly within the range of 2 (Table S2). AIC of models fitted with a Poisson distribution was lower with one exception (Spotted Forktail) (Table S3). We used the model with the lowest AIC to estimate the population and infer the effect of covariates. The c-hat values of the models for individual birds (except Little Forktail, Spotted Forktail and White Wagtail) were < 1 but not << 1, which shows there was no substantial overdispersion or lack of fit in the dataset for most of the birds (Table S2).

3.1 | Estimates of Species Density

Although our study was relatively short term (5 years), there were apparently declines in the absolute abundances of five species of birds (Figure S1). Two were obligate river species (Brown Dipper and Plumbeous Water Redstart) and three were non-obligates (White Wagtail, Common Kingfisher, and White-throated Kingfisher) (Figure 2). Blue Whistling Thrushes showed an increasing trend in population size across the 5 years, while populations of Grey Wagtail, White-capped Redstart, and Crested Kingfisher were stable.

3.2 | Relation of Migration–Immigration and Emigration Across Sites

The arrival rate (γ) was apparently negative for most of the birds (Table S3), but estimates overlapped zero and could not converge in six species most likely due to low counts. The survival rate (ϖ) was positive for all the birds except Spotted Forktail where the estimate could not converge because we encountered few sightings.

3.3 | Effect of Covariates on Estimated Abundance

Elevation was the strongest predictor of abundance for most species (Figures 3 and 4), explaining a significant amount of

TABLE 1 | Individual counts, number of sites, and detection probabilities (with SE) for each species.

Species	Total abundance across 5 years	Sites with at least one non-zero count	Detection probability	SE (detection probability)
Obligate river birds				
Plumbeous Water Redstart (*Phoenicurus fuliginosus*)	674	24	0.866	0.0157
Brown Dipper (*Cinclus pallasii*)	492	28	0.723	0.0257
Crested Kingfisher (*Megaceryle lugubris*)	319	19	0.72	0.0253
White-capped Redstart (*Phoenicurus leucocephalus*)	269	23	0.459	0.052
Spotted Forktail (*Enicurus maculatus*)	98	8	0.568	0.044
Little Forktail (*Enicurus scouleri*)	45	8	0.307	0.049
Non-obligate river birds				
Blue Whistling Thrush (*Myophonus caeruleus*)	423	29	0.666	0.0312
Grey Wagtail (*Motacilla cinerea*)	376	25	0.725	0.0259
White-browed Wagtail (*Motacilla maderaspatensis*)	290	25	0.246	0.035
Common Kingfisher (*Alcedo atthis*)	128	16	0.288	0.0418
White Wagtail (*Motacilla alba*)	109	9	0.322	0.069
White-throated Kingfisher (*Halcyon smyrnensis*)	84	21	0.147	0.041

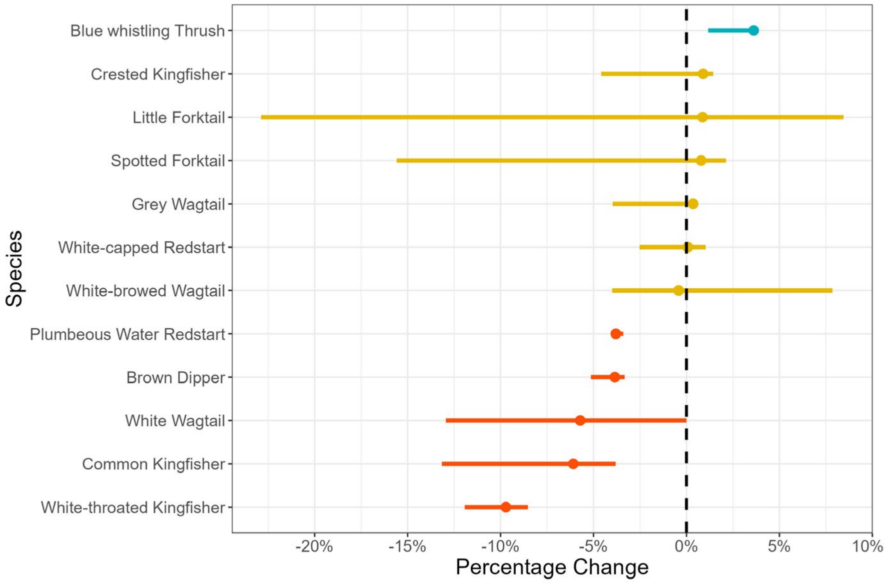

FIGURE 2 | Average population trend of 12 species of birds in the Bhagirathi basin across 5 years (2014–2018). The bars depict 95% confidence intervals of average population density estimate per sampling across 43 sites. Blue indicates increase, yellow indicates a stable population while red indicates a decline in numbers.

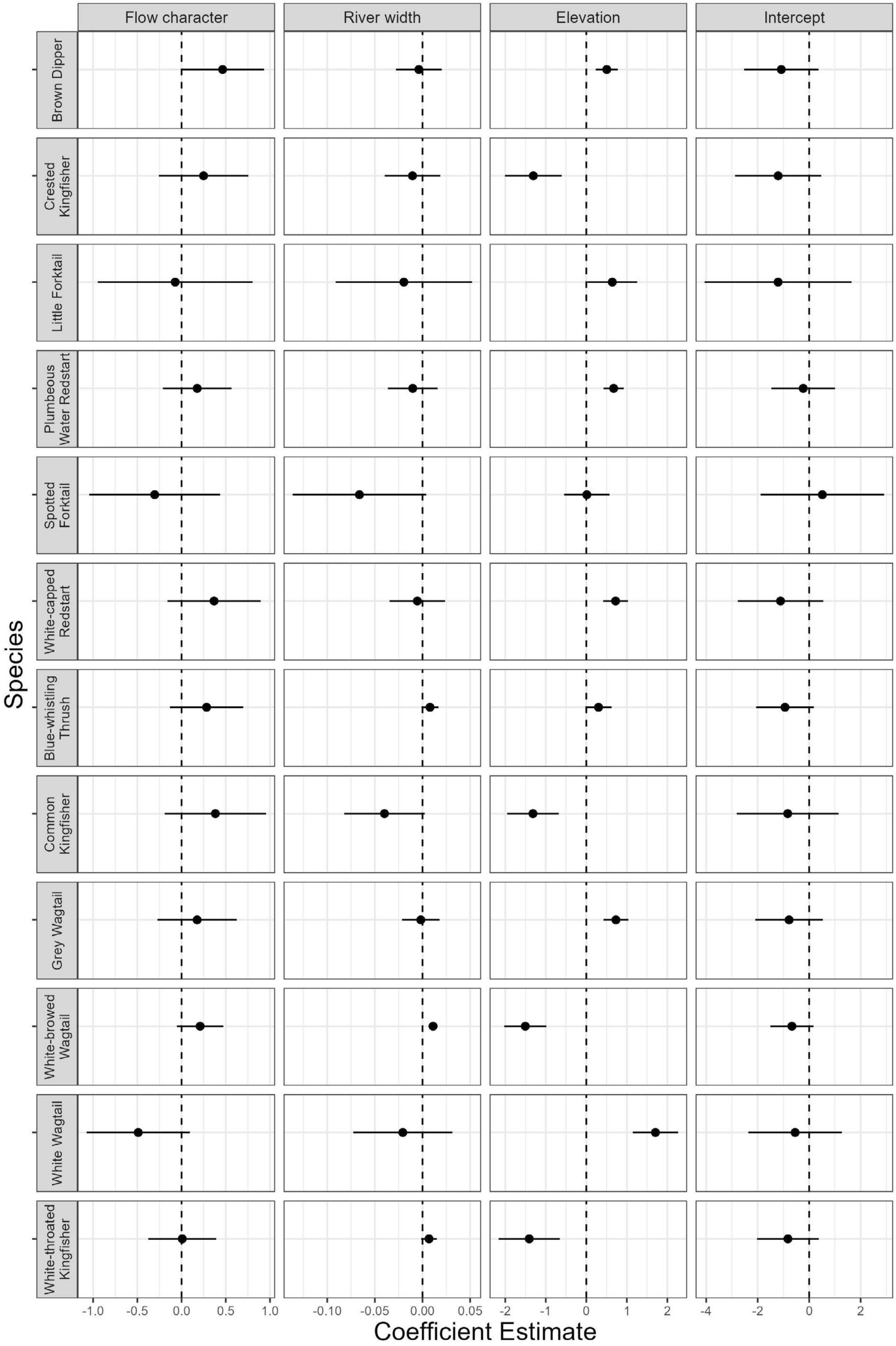

FIGURE 3 | Coefficient estimates of co-variates (flow, elevation, and river width) used to model populations of breeding riverine birds along the Bhagirathi River in an open population N-mixture framework.

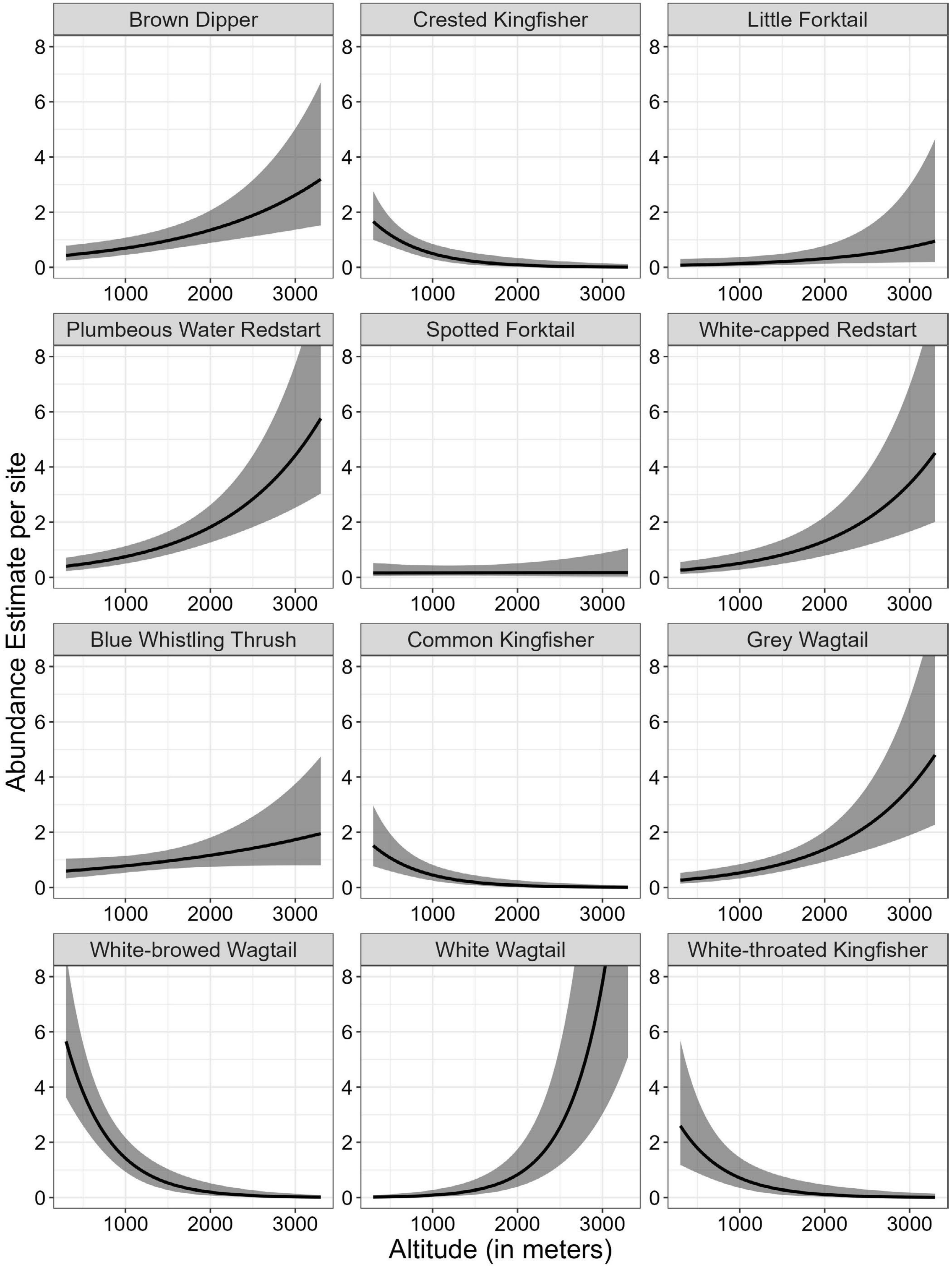

FIGURE 4 | Modeled estimates of abundance per river reach (500 m) for each river bird in relation to elevation.

variation in population size. Riverine passerines such as the Brown Dipper, Grey Wagtail, Plumbeous Water Redstart, White Wagtail, and White-capped Redstart occurred increasingly with elevation over the range of sites studied whereas the Common Kingfisher, Crested Kingfisher, White-browed Wagtail, and White-throated Kingfisher declined (Figure 4). Spotted Forktail showed no significant trend with elevation (Figure 3). River width had a much less pronounced effect on species' abundances (Figure 3). Flow character also had a non-significant effect across the whole community barring the Brown Dipper ($p = 0.052$) which showed a higher affinity toward fast-flowing river sections (Figure 3).

4 | Discussion

Our study is the first attempt to assess effective population sizes and trends of bird species inhabiting riverine environments in the Himalaya based on population density estimates that account for detectability. The outcomes highlight the importance of repeat counts and the value of N-mixture models in estimating abundances of species with linear territories along montane subtropical rivers. Key results illustrate how different species have preferences for habitats over different elevational ranges and illustrate how population patterns can vary even over a relatively short time period—in this case, 5 years. The data also reveal trends among specialized bird species that are consistent with a range of growing local and global threats to rivers in this region (Manel et al. 2000; Sinha et al. 2019). More broadly, the data illustrate how N-mixture models can be applicable to animal population assessment in logistically challenging regions in the tropics and subtropics.

Several key processes affect counts of animals in the field such that models are needed to estimate the abundance of animals accurately (McCarthy et al. 2013). We modeled detection probability to provide density estimates for riverine birds in the Indian Himalaya using possible habitat features established from previous surveys (Sinha et al. 2019; Sinha 2021). The data illustrated how detection probabilities were generally greatest (> 0.5) for obligate river birds, although the White-capped Water Redstart and Little Forktail were less easily detected, perhaps reflecting finer scaled features affecting distribution (Buckton and Ormerod 2008; Sinha et al. 2019). Among non-obligate species, the Grey Wagtail and the Blue Whistling Thrush had detection probabilities > 0.5, reflecting their distribution as conspicuous species along Himalayan headwaters during the summer breeding months (Manel et al. 1999; Sinha et al. 2019). For other species, especially the forktails (*Enicurus* spp.), the numbers of encounters across the duration of the study were limited, perhaps reflecting their association with narrow, fast-flowing streams through forest that were not well represented at our sites (Buckton and Ormerod 2008). There were also lower numbers of White-throated Kingfisher, White Wagtail, and White-browed Wagtails all of which use a wide range of habitats in addition to the river channel. These lower rates of encounter limited inferences about their population trends reflecting models in which important parameters overlapped zero with wide confidence intervals (Table S3). By illustrating the robustness of our modeling framework at such low counts, our study illustrates the importance of field sampling protocols that generate sufficient data to allow model application.

In addition to the need for sufficient data, N-mixture models are sometimes sensitive to various assumptions (Link et al. 2018; Barker et al. 2018; Madsen and Royle 2023). In our data, all bird species (barring three species) produced the best fit using the Poisson distribution model (Table S2) probably because true maximum abundance was relatively close to zero and the number of sites with no individuals was also quite high (Joseph et al. 2009). Dennis et al. (2015) suggested the inclusion of site-specific covariates for a well-defined likelihood surface. We included site-specific covariates that best described the variability across sites where species were detected for modeling the population estimates thus satisfying the N-mixture model assumptions.

For the species that were well represented in the data and well described by the models, high elevation sites had greater abundances of most of the riverine songbirds. This would be expected from the habitat requirements of these species as determined by specific foraging opportunities provided by fast-flowing rivers, geomorphologically complex habitats in the river corridor, and productive environments in regions of high relief (Buckton and Ormerod 2002). For example, modeled abundance estimates showed that Brown Dipper abundance was associated with faster flowing river stretches, a relationship that is uniform across all five species of dippers globally (Tyler and Ormerod 1994). In contrast, lower and mid-elevation sites between 300 and 1600 m a.s.l. were preferred by three species of kingfishers and White-browed Wagtails potentially also reflecting specific habitat requirements. Previous studies have also illustrated strong altitudinal influences on Himalayan river birds, although in our case, the upper survey limit of 3100 m would not have captured distribution patterns for the highest perennial rivers in the region (Manel et al. 2000). As well as fundamental ecological links with natural habitat conditions, altitudinal patterns among river birds might also reflect variations in land use and disturbance from people (Vaughan et al. 2007; Sinha et al. 2019, 2022). Many of these sites have been affected by increasing exploitation for agriculture, hydropower development, and urbanization (Gaur et al. 2019; Sinha 2021). Previous studies in this region have indicated species-specific habitat associations for river birds while also revealing likely effects from anthropogenic change (Sinha et al. 2019; Sinha 2021).

Our data revealed apparent population trends across space as well as through time. Specifically, Blue Whistling Thrushes appeared to be increasing, but five species showed a decline in overall population size of 5%–10% across the duration of the study: Brown Dipper, Plumbeous Water Redstart, White Wagtail, Common Kingfisher, and White-throated Kingfisher (Table 2). While we caution against over-interpreting trends based on a 5-year run of data, patterns for three of these declining species matched long-term and current population trends as revealed by "The State of India's Birds". This national trend is based on data collated entirely from eBird (www.ebird.org/india), a citizen science platform, and includes public observations up till 31 May 2023. As conservation policies and management actions are usually implemented on regional scales (Kamp et al. 2021), this consistency between local and regional-scale data is important. We advocate testing the effectiveness of

TABLE 2 | Population trends of the target species of riverine birds as reported in the State of the Indian birds (https://stateofindiasbirds.in/) population trends for the 12 target species.

Species	Current trend (SoIB)	Long-term trend (SoIB)	Trend from current study
Plumbeous Water Redstart	Decline	Decline	Decline
Brown Dipper	Decline	Decline	Decline
Crested Kingfisher	Decline	Stable	Decline
White-capped Redstart	Decline	Trend inconclusive	Stable
Spotted Forktail	Trend inconclusive	Trend inconclusive	Trend inconclusive
Little Forktail	Decline	Trend inconclusive	Trend inconclusive
Blue Whistling Thrush	Stable	Stable	Increasing
Grey Wagtail	Rapid decline	Decline	Stable
White-browed Wagtail	Stable	Trend inconclusive	Stable
Common Kingfisher	Trend inconclusive	Trend inconclusive	Decline
White Wagtail	Rapid decline	Decline	Decline
White-throated Kingfisher	Trend inconclusive	Trend inconclusive	Decline

our study framework to be extended both in time and to other areas, study systems, and organisms. While longer term data may be needed to confirm the true pattern locally, population declines among river vertebrates are consistent with growing pressures on river environments from multiple sources (McRae et al. 2017). This is especially true in running water systems in tropical Asia where an exceptional riverine biodiversity remains understudied and imperiled by a host of anthropogenic activities (Dudgeon 2000). In the Himalaya, these pressures range from global effects on climate and hydrological dynamics to more local impacts associated with abstraction, pollution, water resources development, and land-use change across the riparian zones and catchment of most rivers (Manel et al. 2000; Shrestha et al. 2012; Sinha et al. 2019). In other parts of the world, studies have reported that habitat specialists often decline at a much faster rate than generalists often with significant conservation impacts (Julliard et al. 2004; Clavel et al. 2011). In the light of these effects of rapid global change, the need to assess population trends is escalating. Yet, it is often challenging to effectively detect trends in species at all spatial scales (Nielsen et al. 2009), and some studies have pointed out contrasting results between different habitats, countries, or regions (Gregory et al. 2005; Riou et al. 2011). Those locations affected by sparse datasets are a case in point and serve to illustrate the value of modeling approaches like ours.

Our study is affected by certain caveats which naturally occur with studies like ours where inferences are drawn based on data collected from the field. Observations were limited to a single river basin and were collected mostly when species were breeding (summer). It may be likely that density estimates in other river basins would vary owing to variations in season or local environmental conditions, river geomorphological features, or adjacent riparian land-use patterns which govern resource availability. We chose to sample during the breeding season as birds are expected to maintain discrete territories at this time of the year. We suggest that future efforts to estimate density should consider the effect of potential seasonal population movements along the elevation gradient as many of the riverine songbirds migrate down to lower elevations during the winter months (Sinha 2021). A further important gap in understanding also arises because the specific foraging niches and prey use of Himalayan river birds are only sketchily understood—yet could offer important insights into their ecology, distribution, and life-history patterns (Maznikova et al. 2024).

Overall, our study provides a design to compare population estimates of riverine birds through time within the same regions or that could be replicated across other montane rivers around the world. The data highlight the role of high-elevation stream systems in sustaining breeding populations of specialized river passerines in the Himalaya mountains. In the regional context, they expand the understanding of the breeding ranges of these lesser-studied species and can be instrumental in detecting and predicting their future range shifts. Mountain ecosystems are under the impact of multiple stressors, particularly degrading water quality, enhanced temperatures, alterations in hydrological cycles, and extreme weather events. These impacts reflect particularly strongly in rivers in the light of large-scale anthropogenic modifications to the riverine habitat. Our study reiterates the significance of extending the monitoring of the long-term population trends of specialist river birds which could benefit the understanding of simultaneous changes in environmental characteristics in riverine habitats. It is noteworthy that birds living in wetland ecosystems are monitored globally owing to their conspicuousness and their established importance as indicators of wetland ecosystems (Kingsford and Porter 2009; Amano et al. 2018; Brandis et al. 2018). In India, however, rivers have not yet been considered in such a scheme of annual censusing. This is ironic as India has a large and diverse network of river systems varying in their geomorphology, hydrological patterns, and assemblages of riverine organisms that are simultaneously vulnerable to a multiple natural and anthropogenic pressures.

Author Contributions

A.S. and N.C. conceived the study; N.C. designed the study; A.S. did field surveys; R.K. facilitated in gaining field permits and funds; and S.J.O. provided overall supervision and writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code to replicate the findings and the analysis of the study can be found at https://github.com/nilanjanchatterjee/Riverbird_pop_dynamics.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.